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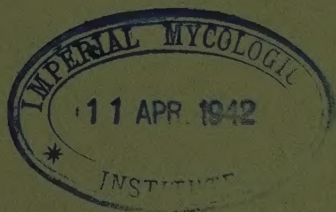
THE BOTANICAL REVIEW

Interpreting Botanical Progress

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CYTOLOGY OF CEREALS¹

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The cereals included in this review are those most commonly spoken of as "small grains," wheat, rye, barley and oat. The first three are members of the tribe *Hordeae* and oat is a member of the tribe *Aveneae*, of the grass family. The chromosome number is 7 or a multiple of 7. Wild forms, known commonly as grasses, are also discussed when used as co-parents with these cereals in hybridization.

Summaries of chromosome numbers (23-26, 114, 115) quickly reveal that purposeful effort in cereal cytology began with the works of Sakamura (97) in 1918. The pioneer work of Kihara (51) in 1919 suggested the possibility that not only chromosome numbers in pure species, but chromosome behavior at maturation divisions in anthers and ovaries might give valuable information toward the solution of puzzling problems in taxonomy and genetics. An increasing wealth of material is made available to the cytologist through greater success in obtaining intergeneric crosses, earlier thought impossible. Weed gardens around the world are scrutinized ever more closely for any wild and little-known cereal or grass that might contribute in some small way toward a better understanding of how nature builds her species and also, possibly, toward the development of economically desirable forms.

Certain improvements in cytological technique, especially in the smear technique, have encouraged more intensive study in chromosome morphology. Cereal chromosomes were considered to be of fairly large size, somewhat long and slender but unfortunately too similar. Kagawa (41), Avdulov (2), Emme (18), Lewitsky (66), Senjaninova-Korczagina (105), and others have devised methods

¹ Contribution No. 52 from the Botany Department of the State College of Washington.

for more detailed observation as to exact size and form, the latter including constrictions, satellites (appendages) and fiber attachments. Some chromosomes of a genom show outstanding individual characteristics and are easily identified, others must be classed in groups of morphologically like chromosomes. One genom, or set of 7, will differ little or much from another set of 7 in respect to individual chromosome morphology, and the degree correlates usually rather favorably with taxonomic and genetic conclusions as to relationships of the plants compared.

Darlington (12-14), Hosono (35), Mather (72), Sax (102), Spier (37, 106), and others have added to the study of chiasmata (locations of supposed chromatid partner exchanges) and their relations to problems of chromosome pairing, and of the, not too well understood but extremely crucial, maturation divisions in general.

WHEAT

The greater part of cytological work in "small grain" cereals has centered about the genus *Triticum*. Much of this work involves also the genera *Secale*, *Aegilops*, *Agropyron* and *Haynaldia*. Taxonomically, the five genera commonly appear together in the sub-tribe *Triticinae* (39) under the tribe *Hordeae*. The possibility of inter-crossing in these genera substantiates the relationships. One species, for instance, has masqueraded under the name of each of four of the genera, as *Triticum villosum* (L.) M. B., *Secale villosum* L., *Agropyron villosum* Lk. and *Haynaldia villosa* Schur. In cytological literature it has been designated as *T. villosum*, but there is a tendency also to retain the genus name *Haynaldia*. Oehler (88) states his preference for *Haynaldia villosa* because several easily recognizable morphological characters distinguish the plant quite definitely from the species of the other four genera.

The chromosome number is known for all 14 to 16 species, subspecies, or races of *Triticum*. The gametic chromosome numbers 7, 14 and 21 coincide with the three taxonomic groups as presented in Flaksberger's classification (20), Percival's wheat monograph (89), Schiemann's general discussion of cereals (104), Watkin's (123) critique on wheat, and other sources. The 7-chromosome or einkorn group is small, including 2 or 3 species with approximately twenty varieties, sometimes referred to as "small spelt."

The 14-chromosome or emmer group embraces 7 to 9 species yielding several hundred forms. The group includes not only "spelts" with brittle rachis and covered grains but several species like *T. durum*, the macaroni and cracker wheat, with grains that thresh naked. The 21-chromosome or vulgare group comprises 4 species which illustrate admirably the results of allopolyploidy, *i.e.*, the combining into one new composite species the genomes (basic chromosome sets) of less closely related species. Vulgare wheat is probably a composite of three such primary 7-chromosome genomes (diagram 1), each of the three genomes differing more or less as to the inherent morphology and physiology of its individual chromosomes from each of the other two genomes. This tripling of building blocks allows ample material, through interplay of dominant and recessive genes, for the rise of various morphological and physiological types, the existence or life of the variants being, in turn, safeguarded by the triplicate genomes. Watkins (123) states that Percival at Reading, England, yearly grows over 1300 varieties of *T. vulgare* alone. The 21-chromosome wheats, with the exception of *T. spelta*, have naked-threshing grains. The varieties of *T. vulgare* of this group are the outstanding bread wheats of the world.

Cytological data are available for over 80 *Triticum* crosses, involving over 40 species or race combinations (1, 23-26, 35, 51, 57, 72, 91, 110, 118, 119, 125). Hybrids within the same chromosome group show comparative regularity of chromosome pairing at meiosis or maturation division, indicating compatibility approaching that of the pure species. The two chromosomes of a pair are usually attached together at both ends forming a ring. Rod-like figures resulting from one end attachment increase in number with the distance of the cross. Unpaired chromosomes in near crosses are found with slightly greater frequency than in the parents. With increase in polyploidy, irregularity in pairing, even in selfed species, increases. Thompson and Robertson (113) observed irregularities, as univalents, in .5-3.4% of pollen mother cells in species of the 14-chromosome group and in 4-4.1% in species of the 21-chromosome group. The frequencies increased in hybrids of these species, varying in the 14-chromosome group from 1.8-26.9% and in the 21-chromosome group from 12.5-42%. Hollingshead (33) found in varietal crosses of *T. vulgare* 5.2-39.1%.

The most common number of univalents was 2 but as many as 8 occurred. Hosono (34) observed rings or irregular chains of 4 chromosomes with conspicuous frequency in some of the 14 chromosome crosses. *T. dicoccum*, in certain hybrid combinations, seems especially conducive toward this irregularity.

Fertility of F_1 hybrids within a chromosome group is usually high, frequently approaching that of the parents (34). An outstanding exception (assuming the exclusion of *villosa* from *Triticum*) is produced by introducing into the crosses the wild wheat, *T. Timopheevi*, recently discovered in Georgia, U. S. S. R. Kihara and Lilienfeld (57) report for these crosses a fertility of 0-4.8%. The small number of ring pairs and other irregularities at meiosis agree with the low fertility. In crosses with the 7-chromosome wheat, pairing approaches 7 which is normal in the triploid cross. It seems that *T. Timopheevi* possesses the *A* genom of the 7- and 14-chromosome wheats but its second genom seems not highly compatible with the *B* genom of the other 14-chromosome wheats. This fact may explain its failure, as yet, to hybridize with the 21-chromosome wheat assumed to contain the genomes *A B C* (diagram 1). Kihara and Lilienfeld suggest the genomes *A G* for *T. Timopheevi*. Cytological findings are in agreement with morphological departures of the plant.

Hybrids between the chromosome groups are characterized by high sterility. The number of pairs at meiosis approaches that of the parent with the lowest chromosome number. The number of probable pairs is most complete, and ring pairs are more predominating in the 21- \times 14-chromosome hybrid (table 1); this hybrid is partly self-fertile (98). The 14- and 21-chromosome groups are apparently more closely related to one another than either of them is to the 7-chromosome group. In other words, vulgar wheat has originated comparatively recently by the crossing of a 7-chromosome form with an emmer which had, in turn, originated through the crossing of two 7-chromosome wheats and had been in existence long before the hybrid now known as *vulgare* arose (diagram 1).

Wild grasses of the genus *Aegilops* have played an extensive rôle in intergeneric hybrids of wheat. Senjaninova-Korczagina (105) writes: "The genus *Aegilops*, which in some of its morphological characters approaches wheat, has proved rather poly-

morphous. Its species, in the majority of cases showing transitional forms, are difficultly classified and grouped into sections. These difficulties of classification have evidently found their expression in the great differences between the systems existing for *Aegilops*. P. M. Zhukovsky, in his monograph on *Aegilops* (1928), establishes 20 species which he arranges in 9 sections. A. Eig (1929) counts 22 species arranging them into 6 sections."

The chromosome numbers as in wheat are 7, 14 and 21. Attempts to make the chromosome groups coincide with taxonomic divisions have not been entirely successful. At least two species have varieties with 14 and 21 chromosomes. Unlike *Triticum*, the 7-chromosome *Aegilops* species are comparatively numerous, approximating 13. There are about 10 species with 14 chromosomes, and 3 or 4 species with 21 chromosomes.

A study of cytological reports (1, 23-26, 42, 43, 56, 75, 90) of 38 hybrids in *Aegilops*, involving 20 different species combinations, forces the conclusion that the genus presents a cytological complexity quite paralleling that of its taxonomy. With rare exceptions, hybrids within either the 7- or the 14-chromosome group have been found to be highly sterile. Pairing at meiosis is spasmodic, ring pairs do not predominate, complexes of 3, 4 or more chromosomes are common. Hybrids between the chromosome groups show but little more irregularity. The study of chromosome charts presented by Senjaninova-Korczagina (105) shows that while species may have many morphologically homologous chromosomes in common, frequently a larger or smaller number is different. On the basis of the types of morphologically similar chromosomes, the species of *Aegilops* may be grouped into sections allying themselves usually with natural taxonomic sections but not with the 7-, 14- or 21-chromosome groups. Within the groups of greatest morphological homology of chromosomes, should be obtained the more meiotically regular, and possibly even a few fertile hybrids; this is exemplified by the hybrid *Ae. speltoides* ($n=7$) \times *Ae. Auchera* ($n=7$), as reported by Kihara and Lilienfeld (56).

Cytological data (1, 8, 10, 23-26, 52, 56, 59, 70, 73, 90, 91) are available for more than 120 *Triticum-Aegilops* crosses comprising over 60 different species crosses. These intergeneric crosses are highly sterile in any chromosome combination (table 1). Meiotic conjugation is feeble, as shown by rarity of ring conjugants, and is

TABLE 1. General summary of chromosome conjugation in F_1 of cereal hybrids. The number (or numbers) in each rectangle represents the most frequent number (or numbers) of chromosome pairs. Numbers occurring in a very high percentage of cells are underlined. The parents in each respective cross are named at the extreme left of the horizontal column and at the extreme top (in abbreviation) of the vertical column in which the particular rectangle is located. The number of unpaired chromosomes may be obtained

	Tr. 7	Tr. 14	Tr. 21	Haynal- dia 7	Hynltr. 21
<i>Triticum</i> ⁷	<u>7</u> ■ ●				
<i>Triticum</i> ¹⁴	<u>4-7</u> □ ●	<u>14</u> ■ ●		<u>0</u> □ ○	
<i>Triticum</i> ²¹	<u>3-7</u> □ ●	<u>14</u> ■ ●	<u>21</u> ■ ●		
(<i>Haynaldtricum Turgidovillosum</i>) <i>Triticum Turgidovillosum</i> ²¹		12 □ ●	14 □ ●		20-21 ■ ●
<i>Aegilops</i> ⁷	<u>2,3</u> □ ○	1-7 □ ○	<u>4,7</u> □ ○		
<i>Aegilops</i> ¹⁴	<u>0-7</u> □ ○	<u>0-6</u> □ ○	<u>0-4†</u> □ ○	<u>0</u> □ ○	
<i>Aegilops</i> ²¹		<u>0-6</u> □ ○	<u>4-7</u> □ ○		
<i>Aegilotriticum</i> ²⁸		13 ●	14 ●		11,12 □ ●
<i>Secale</i> ⁷		<u>0,1</u> □ ○	<u>0</u> □ ○		
<i>Secalotriticum</i> ²⁸					
<i>Agropyron cristatum</i> ¹⁴					
<i>Agropyron glaucum</i> ^{21*}			2-3		
<i>Agropyron glaucum</i> ^{21(?)}			14		
<i>Agropyron elongatum</i> ^{28*}			21		
<i>Agropyron elongatum</i> ^{35*}			10-12		
<i>Avena</i> ⁷					
<i>Avena</i> ²¹					

* Obtained by subtracting 21, vulgare number, from hybrid number.

† Exclusive of *Ae. cylindrica*.

by subtracting the number of single chromosomes represented by the pairs from the sum of the parental numbers. Shaded part of circle within rectangle represents proportion of ring pairs (based usually on authors' statement, in few cases on illustrations only). Shaded part of small square within rectangle represents fertility (unshaded square representing less than 1 per cent fertility). Varietal and specific crosses are inside heavy-lined rectangles, generic crosses outside.

Ae. 7	Ae. 14	Ae.cyl 14	Ae. 21	Aeglt. 28	Sec. 7	Secltr 28	Avena 14	Avena 21	0
		6 □ ○							0 □ ○
		0-3 □ ○							
		7 □ ●							0 □ ○
				11,12 □ ●					
4-7 □ ●		6,7 □ ○							
6,7 □ ○	3-11 □ ●	5-11 □ ●							
	6-9 □ ○								
	13 ●			28 □ ●					0 □ ○
	4-7 □ ○	4-7 □ ○			7 □				
						28 □ ●			
					7 □ ○				
							7 □ ●	4-7 □ ○	
							5-10 □ ○	21 □ ●	

spasmodic and apparently readily influenced by external conditions. The much discussed *Triticum* ($n=21$) \times *Aegilops cylindrica* ($n=14$) cross is a rather outstanding exception in that a mode of 7, mostly ring, pairs are observed at reduction division, suggesting strongly that a genom of 7 chromosomes (set *C*) in *Ae. cylindrica* is homologous with a genom of 7 in vulgare wheat, and that hence these two plants have one 7-chromosome ancestor in common (diagram I). This theory of relationship of *Aegilops* to vulgare wheat has met with considerable criticism, based usually on equally theoretical foundations. However, Senjaninova-Korczagina (105) thinks that the chromosome morphology of *Aegilops* does not speak in favor of its acceptance.

Recently, species of the genus *Agropyron* (or wheat grass) have been considered amenable to hybridization with wheat. The agropyrons are wild grasses, a few sometimes troublesome weeds and most of them serving useful grazing or forage purposes. The chromosome number is known for approximately one-third of the 60 species (7). According to Peto (92), *Agropyron* has attained a polyploidy above that of the "small grain" cereals. Of the cytologically known 7-,² 14- and 21-chromosome species, the majority are in the 14-chromosome group. *A. cristatum* has strains with 7 and 14 chromosomes, respectively; *A. smithii* has strains with 14 and 28, and *A. elongatum* has 35 chromosomes. The report of Sapéhin (100) indicates that a strain of *A. elongatum* possesses 28 chromosomes. Avdulov (2), in his study of chromosome morphology and systematics of grasses, reports finding several types of chromosome sets.

The cytology of interspecific crosses in *Agropyron* is unknown. Cytological study of intergeneric hybrids with *Agropyron* has barely begun. Sapéhin (100) has recently published results of four of these intergeneric crosses. The results are at variance, as table I shows, and Sapéhin explains the discrepancy on the basis of the employment of different biotypes in the two species of *Agropyron*, and offers the comment that the biotypes require more serious botanical and cytological analysis. This initial work will probably open up an interesting and profitable field of investigation.

Haynaldia, according to Bews (7), comprises two species, *H.*

² To simplify presentation the reduced number (in some cases derived from somatic number of original reports) is given.

villosa Schur. from the Mediterranean region and *H. hordeacea* Hack. from Algiers. *Haynaldia villosa* ($n=7$), under the name of *Triticum villosum*, appears in crosses with 14-chromosome *Aegilops* (8) and in this rôle does not cytologically distinguish itself from a 7-chromosome *Triticum*. However, its difficulty in crossing with 7-chromosome *Triticum*, as shown by Oehler's tables (88), and the complete sterility of the cross when acquired, as reported by Sando (98), as well as the almost complete failure in pairing when crossed with 14-chromosome wheat, as found by Berg (5), probably bespeak a more distant relationship to *Triticum*.

RYE

Secale is a small genus with 2 to 6 species including sub-species (7, 104). The outstanding species are *S. cereale*, the bread ryes, and *S. montanum*, a perennial grass. No polyploidy is known in rye and the only deviation from the number 7 is the occurrence in the species of segregates with 8 chromosomes. Belling (3) and Gotoh (29) are of the opinion that the extra chromosome is a segment from one of the largest chromosomes of the normal 7. Lewitsky *et al.* (69) and Hasegawa (32) contend that the 7 chromosomes are the same in both 7- and 8-chromosome rye and that the 8-chromosome rye possesses an extra smaller chromosome with the spindle attachment near one end instead of near the middle. Whatever may be the origin of the smaller chromosome, the frequently unequal distribution of the members of the small pair at meiosis, or according to Hasegawa at the first division in the pollen grain, leads to development of individuals with 14, 15 and 16 somatic chromosomes. Gotoh and also Lewitsky obtained individuals with 18 somatic chromosomes.

Meiosis in the interspecific cross *S. cereale* \times *S. montanum* is regular (70). According to Lewitsky (66), the chromosome morphology of *S. montanum* is similar to that of *S. cereale*. One pair of chromosomes is distinguished by satellites, the other by size and comparative length of the two arms. Of the approximately 30 intergeneric crosses involving 12 different species combinations, the largest number is with *Triticum* (1, 8, 9, 21, 23-26, 43), 5 crosses are with *Aegilops* (4, 43) and one, recently reported by Favorsky (19), is with *Agropyron*. If the degree of pairing is a true test, *Secale* is more closely related to *Aegilops* and *Agropyron*

Primary species

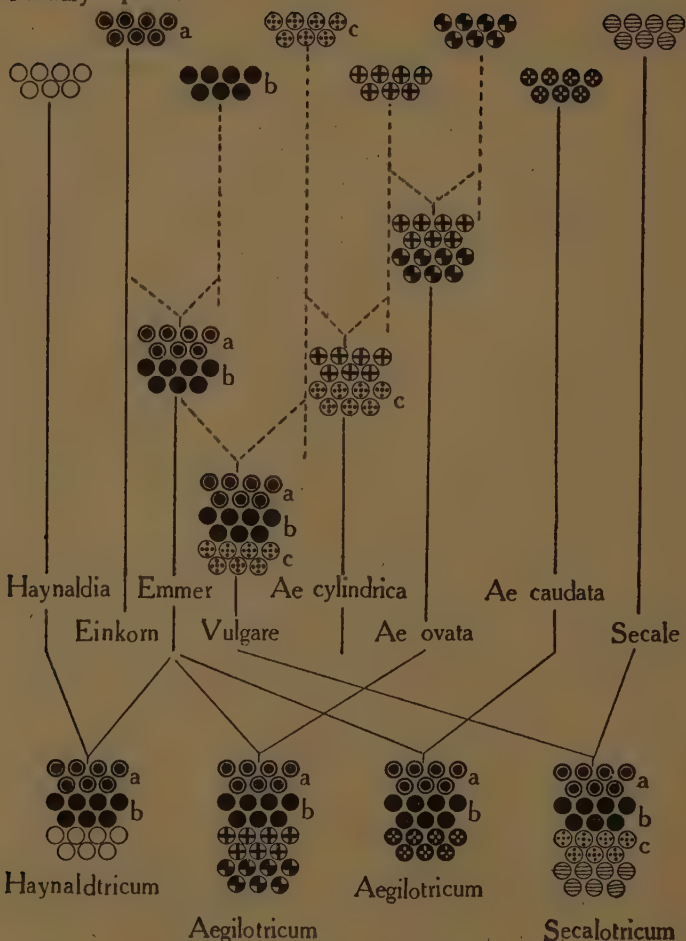


DIAGRAM 1. Allopolyploidy in wheat. Symbols indicate immediate origin of each set of 7 chromosomes. Thus in *Secalotricum* chromosome sets a, b, and c are identical with sets a, b, and c of its vulgare parent, while the remaining set is identical with that of its rye (*Secale*) parent. When back crosses have been made as in case of *Haynaldtricum* and *Aegilotricum* (table 1), the number of chromosome pairs has been found to approximate rather closely to the number of chromosomes in the hybrid that find identical partners in the parent with which it is back crossed. Unbroken lines represent the formation of amphidiploids, or new species (4 plants near bottom of diagram), through very recent artificial hybridization. Broken lines indicate hypothetical formation of species as found in nature, through possible natural hybridization. These hypotheses as to the origin of the natural species and suggested by pairing behavior in artificial crosses are not fully accepted by all research workers in the field.

than to wheat. Favorsky comments in respect to the *Triticum-Agropyron* cross that the 7 pairs, including ring forms, indicate a certain degree of relationship between rye and *Agropyron cristatum*.

BARLEY

The chromosome number has been ascertained for the majority of the approximately 25 species of *Hordeum*. Most of the wild species and all the cultivated varieties have 7 chromosomes. From man's viewpoint the genus *Hordeum*, in contrast to *Triticum*, has not been improved through polyploidy. Three species of *Hordeum* have 14 chromosomes, *H. murinum* and *H. jubatum* are both credited with 7 and with 14 chromosomes, and *H. nodosum* with 7 and with 21. Possibly, as in *Aegilops*, these species may comprise races or varieties which differ in chromosome numbers. The chromosome morphology is presented by Ghimpu (27), Lewitsky (66) and others. Two pairs of chromosomes are distinguished by satellites in varieties of the 7-chromosome barleys, *H. vulgare* and *H. distichum*, according to Lewitsky. The cytology of meiosis of *Hordeum* hybrids is not known.

OAT

Malzew (71), in his recent revision of the genus *Avena*, gives 7 species and 22 sub-species. The chromosome number is known for most of the species and many of the sub-species. Several species have 7 chromosomes. *A. strigosa* includes sub-species with 7 and with 14 chromosomes. The more important agricultural forms are included in the two species and 14 sub-species with 21 chromosomes. Increase in polyploidy has greatly increased polymorphism as to number of forms, bringing about a contrast to the extreme poverty of forms in the 7-chromosome species. Emme (18) finds considerable size variation in *Avena* chromosomes. Comparative arm lengths of chromosomes, more rarely appendages, assist in the comparison of genomes of different species.

Reports are published on 17 interspecific crosses of *Avena*, including 13 different species or sub-species (23-26, 17, 80, 84, 86, 94). The 21- \times 21-chromosome crosses show comparatively few irregularities, in the form of unpaired chromosomes and trivalents, and have a fertility equal to that of the parents. Crosses involving

unequal numbers in parents are highly sterile. In contrast to *Triticum*, pairing in a 14×7 cross is more regular, with more ring conjugants, than in 21×14 . The 21×7 cross gives fewer ring conjugants than the comparable combination in *Triticum*. The 21-chromosome *Avena* species, apparently closely related *inter se*, are more distantly related to the 14- and 7-chromosome species thus far used in hybrids. The 14-chromosome species are probably of more recent origin through the crossing of two 7-chromosome species. The 21-chromosome species, on the other hand, have originated from a more ancient 7×7 -chromosome cross which later combined with a 7-chromosome species. Malzew (71) presents a diphyletic scheme giving a separate origin to the 21-chromosome section. The substitution of other 7- and 14-chromosome species in the above crosses, and also crosses within the 7-chromosome group as well as within the 14-chromosome group, may give added cytological information.

HYBRID OFFSPRING

The presence of univalents and other irregularities during maturation divisions gives rise to pollen grains and embryo-sacs of varying chromosome numbers. Even close hybridization tends, however slightly, to disturb chromosome balance in the offspring. In crosses involving different chromosome numbers in parents, and maximum pairing, as in the 21×14 -chromosome wheat cross, the maturing F_2 individuals lie too predominantly within one or the other of the parental chromosome groups, and the variants from the parental numbers are further eliminated in succeeding generations. Occasionally, stable lines are found with an intermediate chromosome number or with one chromosome more or less than a parental number. Sometimes the addition or loss of a chromosome manifests itself by some morphological character such as dwarfness (60). Some speltoids and compactoids of wheat and fatuoids of oats are brought out by the loss or gain of a particular chromosome.

Considerable study has been directed toward cytological aspects of dwarfs, speltoids, compactoids and fatuoids in general (31, 36, 37, 81, 85), and theories have been proposed as to the cause and origin of the various types of segregates.

Several factors seem to encourage reversal to parental chromo-

some numbers in hybrid offspring. Thompson and Armstrong (111) found in the 21×14 -chromosome wheat cross that pollen grains with intermediate chromosome numbers are retarded in their nuclear development and this is again correlated with a deficiency of cytoplasm. "Unfavorable chromosome conditions in grains with intermediate numbers cause a complete abortion of some grains and retardation of nuclear development in others. Under the best available experimental conditions only 11 or 12% of F_1 pollen grains germinate, in contrast to 70 or 80% for parental pollen. No grains with reduced cytoplasm germinate, and at least 50% of those with apparently normal cytoplasm fail to germinate." A large percentage of the apparently normal F_1 pollen grains fail to germinate on the F_1 stigmas, apparently the result of mutual unfavorable relationships of F_1 pollen and F_1 stigmas. Parental pollen germinates equally well on parental and F_1 stigmas. Thompson (108), in order to determine the causes for wrinkled endosperm, back-crossed the F_1 of 21×14 -chromosome wheat crosses with emmer ($n=14$) or vulgare ($n=21$) pollen. By counting chromosomes in the offspring, he calculated the chromosome number in the nuclei in the functioning embryo-sac. He concluded that the endosperm condition is dependent on the extra 7 vulgare chromosomes in the triple fusion nucleus. It is plump when the extra 7 are absent or are in complete or almost complete duplicates or triplicates, *e.g.*, $(14+14)\text{♀}+14\text{♂}$, or $(21+21)\text{♀}+14\text{♂}$, or $(21+21)\text{♀}+21\text{♂}$. It is shriveled when the extra 7 are haploid, *e.g.*, $(14+14)\text{♀}+21\text{♂}$ or are diploid or triploid for a few only. "The farther the chromosome situation departs from the complete absence or complete diploidy or triploidy of the vulgare chromosomes, the severer is the shrivelling. Endosperm conditions, depending in this way on chromosome conditions, play a large part in the non-appearance of many types in F_2 and later generations of ordinary crosses." Wakakuwa (122), in a study of the F_1 embryo development in wheat, concludes that embryos of all combinations between species with different chromosome numbers are smaller than those of the mother selfed. Growth of the embryos is always better if the female is the high-chromosome plant than in the reciprocal. Development of hybrid seed depends upon growth of both the embryo and endosperm, which depends, in turn, upon the numerical chromosome relationship of the sperm nucleus to the egg

and polar nuclei, respectively. Katayama (45), in a study of compatibility in reciprocal crosses of wheat and *Aegilops*, concludes that there is a qualitative as well as a quantitative chromosome relationship that determines development of the hybrid seed, and that the qualitative shows up more definitely the more remote the cross. Kihara and Wakakuwa (53, 61, 62), Nishiyama (84) and Watkins (123) offer more extensive discussions on fertile and sterile combinations relative to formation of hybrid offspring.

Some F_1 hybrids, like wheat \times rye, are apparently completely pollen sterile. The anthers are poorly filled with irregular and a large percentage of abortive pollen grains and do not open. From these hybrids progeny may be obtained by back-crossing. In such cases, the chromosome number tends to stabilize when it acquires the chromosome number of the pollen parent.

In general, it seems that the fewer the conjugants in the meiosis of a hybrid the greater is the tendency for the offspring to attain, or even to far exceed, the chromosome number of the highest-chromosome parent, or, if the parents have the same number, to waver between the parental number and the sum of the parental numbers.

This brief presentation can merely suggest the general cytological trend in hybrid offspring. A longer list of literature is available than can be included (9, 21, 30, 76, 77, 95, 96, 112, 121, 125) and many articles represent more intensive study in the field of genetics.

AMPHIDIPLOIDS

The term amphidiploid has been applied to hybrid offspring arising through doubling of each genom of the F_1 hybrid. All amphidiploids thus far known have developed from crosses showing few, if any, conjugants in the F_1 . They are of interest in that they give us one illustration of how new species, especially allopolyploids, may be obtained. The new forms are comparatively fertile, in most cases quite stable, and combine characters of the two parents, a feat not readily accomplished between wide crosses. Pairing is not so regular as in either of the two parents. Whether this irregularity will gradually give way to regularity remains for time to determine.

The first two amphidiploids were described in 1926 by Tschermak and Bleier (117) as occurring in the F_5 and F_6 progeny of *Ae. ovata* ($n=14$) \times *T. dicoccoides* ($n=14$) and *Ae. ovata* \times *T. durum*.

They were named *Aegilotriticum forma fertilis* No. 1 ($n=28$), and *forma fertilis* No. 2 ($n=28$), respectively. Percival (90) in 1930 discovered another octoploid in the F_2 of *Ae. ovata* \times *T. turgidum*, and Kihara (54) in 1931 discovered still another in the F_2 progeny of *T. dicoccoides* \times *Ae. ovata*, and in 1934 Oehler (87) reported 3 octoploid individuals found in the F_2 of *Ae. triuncialis* \times *T. dicoccum*. He named the new form *Aegilotriticum triuncialis-dicoccum* ($n=28$). Oehler, in the same contribution, described some hexaploid amphidiploid plants found in the F_2 of the triploid cross, *Ae. caudata* ($n=7$) \times *T. dicoccum* ($n=14$), and suggested for this constant form the name *Aegilotriticum caudatadicoccum* ($n=21$). The first amphidiploid hexaploid was described by Tschermak in 1930 (116). It occurred in the F_2 progeny of *T. turgidum* ($n=14$) \times *T. villosum* (7) and was named *T. turgidovillosum* ($n=21$), but as it involves the much cast about species *villosum*, Tschermak suggests also the name "*Haynaldtricum*" *turgidovillosum*. Its cytology has been reported in detail by Berg (5, 6).

In wheat-rye progeny several amphidiploids have developed. The first was referred to by Meister in 1928 (74) as appearing in the F_2 of *T. vulgare* ($n=21$) \times *S. cereale* and was described cytologically by Lewitsky and Benetzkaja (68) in 1931. This form has been referred to as "*Secalotriticum Saratoviense*." Lebedeff (65) in 1934 reported several amphidiploids occurring in the F_2 of vulgare wheat \times rye following an attempted back-crossing with rye pollen. Lebedeff suggests apomixis as a possible method of origin.

Berg (5) crossed the amphidiploid *Aegilotriticum* ($2n=(14+14)_2$) with the amphidiploid *T. turgidovillosum* ($2n=(14+7)_2$) obtaining, thereby, a quadruple hybrid, involving 4 species, and 3 genera if *villosa* is considered as a species of *Hanaldia*.

Many suggestions have been proposed as to the method of origin of amphidiploids. It has been proved for the majority of the above cited amphidiploids that they have arisen not later than in the F_2 generation, and they have probably had their origin in the ovule of F_1 , or fertility would have led to their detection in F_1 . The most frequently offered suggestion is the fertilization of an unreduced egg by an unreduced male gamete. The unreduced gametes developed probably as a result of failure of the first reduction division, the second resulting in the splitting of all the chromosomes, thus

forming 2 unreduced instead of 4 reduced cells. That such unreduced eggs are developed has been rather definitely demonstrated. Meiotic figures, indicating failure of the first reduction division, have been frequently observed. More direct evidence is probably offered by back-crossing or by pollinating F_1 with known pollen and thus calculating the chromosome number of the F_1 egg.

Katterman (49), in back-crossing the F_1 of wheat-rye hybrids with vulgare pollen, ascertained by counts in 50 F_2 plants that the functioning egg in F_1 contains from 11 chromosomes below to 3 above the somatic number of the F_1 and that the percentage of unreduced functioning ♀ gametes is high. Kostoff (63) pollinated the F_1 *T. (dicoccum × monococcum)* with *T. vulgare* pollen and obtained two plants with the somatic chromosome number 42, or $(14 + 7) + 21$. Müntzing (78) obtained a similar type of hexaploid, but with rye as the 7-chromosome parent in F_1 . That unreduced female gametes are not infrequently produced seems evident. The question still remains unanswered as to the accomplishment of fertilization when the anthers of the hybrid so persistently fail to open. It has not been proved, however, that the anthers or parts of them never open. Katayama (47) in 1935 observed anthers discharging pollen grains in a haploid *Aegilotriticum*. Amphidiploids, in fact, arise comparatively infrequently, or at least sporadically. Katterman (50) proposes simultaneous fertilization of the unreduced ♀ gamete by ♂ cells from both parents. Kihara and Lilienfeld (58) observed nuclear migration in young pollen mother cells and raise the question as to the possible relation of nuclear migration to polyploidy in pollen grains, but are aware of the preclusion of such phenomena in the single spore mother cell of the cereal ovule. Nishiyama (84) suggests doubling of chromosomes after fertilization as the origin of several autotetraploid plants found in F_4 segregates of a 14×7 -chromosome *Avena* cross.

Aside from the usual type of chromosome segregates and amphidiploids in hybrid offspring, there occasionally occur other fertile forms. Some of these are characterized by deletion of apparently entire genomes. Kostoff (64) found in F_1 of *T. vulgare* ($n=21$) \times *T. monococcum* ($n=7$) a fertile plant with 35 somatic chromosomes and assumed that the *vulgare* was pollinated with an unreduced *monococcum* ($n=7$) sperm. At meiosis, the 14 *monococcum* chromosomes formed 7 pairs and the *vulgare*, as interpreted

by Kostoff, pairing *inter se*, formed 5–10 more pairs. The subsequent generation had 28 chromosomes through elimination of 7 extra *vulgare* chromosomes. Nishiyama (83) discovered a diploid ($n=7$) in the progeny of a 42-somatic-chromosome ($17_{11}+8_1$) plant derived from *Avena fatua* ($n=21$) \times *A. barbata* ($n=14$) cross. The autodiploid was in part like the tetraploid parent. It crossed readily with 7-chromosome *Avena* species. Dusseau (15) observed in the F_2 of an intervarietal *vulgare* ($n=21$) wheat cross a plant with characters of durum ($n=14$) but with the chromosome number of *T. monococcum* ($n=7$). He proposes the name *T. haplodurum* and suggests that the plant confirms the existence of a common gene in *T. vulgare* and *T. durum*.

HAPLOIDS

Until recent years, haploids or parthenogenic plants were unknown in angiosperms. Due to irregular distribution of unpaired chromosomes at meiosis and resulting sterility, haploids are of very temporary existence, unless they are capable of vegetative propagation.

The first haploid in cereals was described by Gaines and Aase (22) in 1926. This plant arose following pollination of *T. compactum* ($n=21$) with *Ae. cylindrica* ($n=14$) pollen and, no doubt, resulted from parthenogenetic development of the *T. compactum* egg cell. Pairing at meiosis was practically absent, the univalents segregating by chance to the two poles. Indications of non-reduction were noted. The plant was normal *T. compactum* except that it was highly sterile. The few seeds gave rise to normal $2n$ plants. Yamasaki (124), in strains derived from varietal crosses of *T. vulgare* ($n=21$), found 3 plants, smaller in size and highly sterile. Root-tip counts proved them to be haploid.

Chizaki (11) in 1934 found a haploid plant in offspring from seed produced by retarded spikes of *T. monococcum* ($n=7$) in a field in bloom at high temperature (32° – 34° C.). Chizaki proposes the following causes of its origin: (1) “. . . the high temperature acts as a physical stimulus on the egg cell to start in the parthenogenetic development; (2) the pollen or pollen tubes lose their fertilizing ability owing to the high temperature, but they stimulate the egg cell to develop to haploid plant; (3) by the influence of high temperature the egg cell was injured and the male nucleus

developed merogonously." Kihara and Katayama (46, 55) in 1932 discovered 3 haploids in *T. monococcum*. One arose voluntarily in a pure line of bagged plants, the other two as results of X-raying spikes at the reduction division stage. The authors suggest parthenogenetic development of the unfertilized egg. As in the 21-chromosome haploid, there was no pairing at meiosis. The plants were smaller than the diploid *monococcum*. One seed gave rise to a normal diploid plant. Katayama (46) found that haploid plants appeared in a field of ordinary culture to the extent of .48%, indicating that egg cells of *T. monococcum* can develop parthenogenetically. When spikes at stage of meiosis were X-rayed, the haploids increased to 5.26%; if pollinated, the number increased to 7.41%. If spikes with mature pollen were X-rayed and pollen from these spikes transferred to untreated pistils, emasculated 3 days before, the number of haploids rose to 17.58%. Untreated pollen transferred to X-rayed pistils gave no haploids, showing that germ cells cannot be activated to develop embryos by exposure to X-rays. Katayama states: "Generally, it is considered that some male nuclei derived from pollen or PMC which was X-rayed degenerate without fusing with egg nuclei, if they entered the ovule. But, by the stimulation of male nuclei, egg nuclei may have been activated to develop parthenogenetically. It may be conjectured also that the endosperms developed through either the similar process in the egg or normal triple fusion."

Namikawa and Kawakami (79) observed rather frequent occurrence of twin seedlings in F_3 and F_4 generations of *T. vulgare* varietal crosses, and learned further that the twins were not always identical as to chromosome number. In 19 grains both plants were normal autodiploid ($2n=42$); in 8 grains, one plant was autodiploid and the other autotriploid ($2n=63$); in one grain, one plant was autotriploid and the other autotetraploid ($2n=84$); and finally, in one grain one plant was autodiploid and the other haploid, containing only 21 chromosomes in root-tip nuclei. Fertility of the autotetraploid was 80.5%, of the autotriploid 0.4–47.2%, and of the haploid 2%. The authors do not comment on the method of origin. The rise of autopolyploids suggests the possibility of a similar origin of amphidiploids. Johansen (40) found about 10% of haploid seedlings in a commercial lot of grains of *Hordeum*.

The antithesis of haploids and amphidiploids is well illus-

trated by the appearance of two haploids from seeds of bagged spikes of *Aegilotriticum* ($n=28$), as described by Katayama (47). One plant was slightly hypohaploid in that it had lost the greater part of one chromosome. This deficiency seemed to express itself morphologically in a slightly reduced spike. Katayama describes the meiosis as similar to that of the original F_1 (*T. dicoccoides* \times *Ae. ovata*), but the number of conjugants was smaller, and non-reduction in the form of restitution nuclei was more frequent, resulting in a larger proportion of plump pollen grains in the haploid, especially in the hypohaploid individual.

CHROMOSOME CONJUGATION

Table I gives a bird's-eye view of cereal crosses cytologically studied. It represents a very general summary of over 300 crosses, involving more than 150 different species combinations. An attempt has been made to record the most dominating mode. The original data represent observations of plants grown under frequently different ecological conditions in countries far removed from one another. The results are comparatively uniform, with most deviations apparently resulting from use of different varieties.

The value of chromosome conjugations at meiosis of hybrids as a measure of relationships has recently been discussed by Sax (103).

A few experimental data in cereals, illustrating how various factors may influence instability of conjugation, will be cited. Katayama (44), in a statistical study of a wheat-*Aegilops* cross, found that number of conjugants is not influenced by direction of the cross nor by selection of individuals. Diurnal and seasonal variations he attributes to temperature. In plants kept at lower temperatures, as 6° and 15° C., for twelve hours, meiosis was normal except for occasional massing of a few chromosomes; at about 25° C. the number of conjugants began to decrease; and at the highest temperature (38° C.) the division was greatly disturbed and bivalents could not be observed. Peto (93) induced chromosome aberration, in the form of fractures, by high temperature treatment of barley seed. This primary result will lead to meiotic aberration if fractures are permanent or if resulting fragments are transposed to other chromosomes as observed. Peto states that: "Importance is attached to the discovery that a large proportion of

the mutant cells are eliminated during growth of the plant. The principle that only the fittest survive seems equally true of cells as of individuals and groups of plants or animals."

Results of X-ray treatment manifest themselves in many types of aberrations. Translocations of chromosome parts and resultant altered chromosome morphology were observed by Lewitsky and Araration (67) in *S. cereale*. Katayama (48), in *T. monococcum*, conjectured that a small part from one chromosome grafted to the end of another led to formation of an open ring of 4 chromosomes. Manifestations in the plant were slenderness, lowered fertility (about 36%) and poor germination. In polyploid wheats, where vital genes may be duplicated in several genomes, the effect on the morphology and physiology of the plant may not be apparent. According to Stadler (107), ". . . seedling mutations are common in *Triticum monococcum* with 7 pairs of chromosomes, much less common in *T. durum* with 14 pairs, and rare in *T. vulgare* with 21 pairs." From Tascher's data quoted by Stadler, "irradiation induces partial sterility with high frequency in *T. monococcum* but the frequency is much lower in *T. durum*, and extremely low in *T. vulgare*."

While mutations may not find as ready expression in polyploids, the chromosome homology and pairing will probably be disturbed equally as much as in the monoploid. Sapéhin (99), in X-rayed *T. spelta*, noted, besides various chromosome aberrations, the absence of conjugants.

Pairing irregularity increases with increased polyploidy, as illustrated in wheat. Amphidiploids are characterized by considerable irregularity at meiosis although each chromosome apparently has an homologous mate. We do not know the exact cause for these irregularities and we do not know that they will completely disappear with time.

There are also some evidences in cereals of genic control of conjugation. Ekstrand (16), in a two-rowed barley, *Hordeum distichum* ($n=7$), found some sterile or partially fertile plants showing asynapsis of some of the 14 chromosomes. Huskins and Hearne (37) found that absence of the *C* chromosome pair of fatuoid oat dwarfs was accompanied by failure of chromosome conjugation and consequent sterility. He thinks that the *C* chromosome carries the gene for pairing. The factor is so nearly domi-

nant that absence of only one of the *C* chromosomes, as in the 41-chromosome (somatic) plant, results in only lowered chiasma frequency. Asyndesis was found also in the 40-chromosome (somatic) dwarf speltoid wheats. Nishiyama (81, 85) found in *Avena fatuoids* ". . . that the long arm of the *C* chromosome (s_1) contributes to normal pairing and its short arm (s_2) to the cultivated characters of the grain."

EXPLANATORY NOTES

Every vegetative cell of a plant possesses chromatic material in its nucleus which is exhibited in a certain constant number of chromosomes at cell division. Among cereals this number ($2n$) is usually some multiple of 7. When sex cells are formed at meiosis (reduction division) they receive only half this number (n). At fertilization the number is again doubled. According as a plant contains n , $2n$, $3n$, $8n$, etc., number of chromosomes in its body cells it is known as a haploid, diploid, triploid, octoploid, etc., respectively. Plants with higher multiples are known as polyploids. When these various classes form sex cells (gametes) the chromosomes appear, at a certain stage of the reduction division, singly (univalents), in pairs (bivalents), in triplets (trivalents), etc. The chromosomes which are thus associated in groups are homologous to one another, *i.e.*, each is derived from a different parent but all influence the same characters. The influence of one or more of each group may be dominant over the others (recessive) with respect to some feature.

As they are borne on the plants, the grains or fruits of cereals are surrounded by small scale-like leaves. In so-called covered grains these surrounding bracts are not removed by threshing; in naked grains they are.

allopolyploid: a polyploid whose chromosomes do not usually form multivalents at meiosis but pair as far as their homologies allow them (Darlington).

a polyploid possessing unidentical sets of chromosomes derived from two or more plants of dissimilar origin.

Allopolyploids contain a complement of chromosomes derived from two or more plants of dissimilar origin, and it is upon the degree of similarity between these two or more kinds that the type of pairing and disjunction of the chromosomes and

- hence the segregation of factors depend. (Sansome and Philp).
- amphidiploids: plants showing the exact doubling of each chromosome of the F_1 hybrid from which they have been derived, *i.e.*, plants possessing the sum of the somatic numbers of both parents of the hybrid.
- apomixis: development of an individual from an unfertilized egg without sexual fusion, whether the egg be normally haploid, or abnormally diploid through failure of reduction division.
- asynapsis: failure of homologous chromosomes to occur in pairs during reduction division.
- asyn-desis: asynapsis.
- autodiploid: a plant possessing two identical sets of chromosomes.
- autotetraploid: a plant possessing four identical sets of chromosomes.
- back-cross: cross-pollination between a hybrid and one of its parents.
- biotypes: distinct physiological races or strains within morphological species.
- chiasma(ta): fusion of homologous chromosomes at one or more points.
- compactoids: mutants occurring in cultures of common wheat, *Triticum vulgare*, and possessing characters of *Triticum compactum*, club wheat.
- conjugants: paired or otherwise joined chromosomes.
- endosperm: the food-storage portion of a seed which nourishes the embryo. Its tissue is triploid ($3n$), resulting from fusion of one male with two female nuclei.
- fatuoids: mutants occurring in cultures of cultivated oats and possessing the characters of *Avena fatua*, wild oats.
- fiber-attachment: spindle-attachment, the point on a chromosome joining the "spindle-fiber" and proceeding first to the pole during anaphase.
- genom: the entire number of chromosomes inherited as a unit from a parent.
- hypohaploid: plant with slightly less than haploid chromosome number.
- merogony: development of an embryo from a portion of an egg without the functioning of the egg nucleus; sperm nucleus only develops.

non-reduction: reception by sex cells of the vegetative number ($2n$) of chromosomes rather than half the number ($1n$).

PMC: pollen-mother-cell.

restitution nucleus: a single nucleus formed with an unreduced number of chromosomes in place of two nuclei with reduced chromosome numbers where reduction division should occur.

satellite: a segment of a chromosome, terminal or intercalary, separated from the rest by one or two very narrow constrictions.

speltooids: mutants occurring in cultures of common wheat, *Triticum vulgare*, and possessing characters of *Triticum spelta*, spelt wheat.

translocation: transfer of a segment of a chromosome to another part of the same chromosome or to a different chromosome.

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THE RELATION OF WEATHER TO FUNGOUS AND BACTERIAL DISEASES

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The subject of the correlation of weather to plant diseases has long been recognized as of considerable importance and, for some years past, research has gradually elucidated some of the factors involved in the causation of epidemics, many of which have serious economic consequences. "Weather" is rather vague but is useful as a collective term covering innumerable factors.

There seems little point here in entering into a long description of the many factors involved in the term "Weather" and the various ways in which these factors influence the disease complex. There are many excellent papers which survey this subject from various viewpoints (12, 13, 48, 89) and the writer in 1929 gave a brief summary of the more important work which had been carried out up to then (33). Since then Wilson (124) published a rather comprehensive bibliography, with a subject index, which has fulfilled a very useful function.

GENERAL

Investigations on this subject prior to 1920 had not probed fundamental issues and in many cases much labor was expended in an attempt to correlate the whole weather complex with disease incidence without reference to the separate factors. However, it was soon realized that the weather-disease complex could not be understood until the separate meteorological factors comprising "Weather" had been fully analyzed and their influence on disease studied one by one. The first outstanding and well organized research on each meteorological factor in relation to disease was started at Wisconsin, using apparatus by which the factors could be automatically controlled (54, 56 and lit. cit. in 33). Detailed knowledge of the way fungi and bacteria were influenced in the attack on their specific hosts was rapidly obtained both at Wisconsin and at other centers, while parallel work continued on the influence of the same factors on the growth of the organisms concerned, a work which had been carried on for years without realizing its true significance in the etiology of disease. Jones and his

colleagues investigated also the conditions of growth of the host plants and found that where the range of a factor was common to both host and disease organism, there the disease could be expected in most cases (55). This phase of etiological research was mirrored in the new presentation of these facts in the textbooks which, previously, had been more concerned with taxonomy and symptomatology. Views have changed very much and it is being recognized better that no true knowledge of a disease problem can be obtained without taking into consideration every etiological factor. Etiology has been considered too narrowly as concerning the immediate and apparent cause, the parasitic agent, instead of the vast field really involved. Even though such factors as temperature, moisture, light and wind are recognized as influencing disease incidence and progress, it seems that these same factors in a year preceding the season concerned, the total past history of the plant, its genetical and physiological constitution, and other factors are much less readily recognized as playing a truly significant part in the final causation of disease. Various writers have protested against the narrow view of etiology and a better conception of this subject is to be found in Link's (59) recent paper. He rightly draws attention to the need for investigating the physiology, culture and genetics of a plant in health jointly with that of the diseased state. External and internal factors may cause disease directly without any interference of a living disease agent, such as insect or fungus; it will be necessary for the investigator of a fungous or bacterial disease to keep this subject in mind. What the writer would prefer to call the "ecological" factor in the etiology of a disease is often ignored, though quite well known. This "ecological" factor would define the relationship between the natural habitat of a plant, *i.e.*, xerophyte, hydrophyte, etc., and that in which the plant was found with a disease, an especially important point when the plant is grown for economic purposes. Jarvis (48) has also suggested that a study of ecological conditions as related to crop production would yield a better understanding of the incidence and control of plant diseases.

EPIDEMIOLOGY

One of the most important points when investigating epidemics of plant diseases is that of the measurement of disease. As pointed

out by Moore and others (33, 61, 71), any human estimation of disease intensity is very unreliable when there is no standardization of degrees of infection. Even two individuals who have worked in conjunction on the same disease will each arrive at a different estimate of the percentage of disease. For apple scab (*Venturia inaequalis*), Moore, in England (71), has worked out a "category" method of estimating damage, which has the advantage of being formed on a statistical basis, comparisons between affected trees being reasonably sound. In America, charts for various rusts have been in use for some time, showing the standard degrees of infection (10). An interesting point of much importance is the difference between "extensity" and "intensity" of disease; "intensity" has in the past incorrectly covered both meanings. In only a few cases may measurement of "intensity," *i.e.*, severity in unit infection, represent also "extensity," *i.e.*, distribution of infection (5). In the measurement of epidemics this difference will have to be more considered than in the past.

ANTECEDENT FACTORS

There are many factors which influence disease epidemics considerably in advance of the event, only a limited number of which can be mentioned:

1. Weather generally determines to a very large extent the production of fungus spores in the summer season and it is on this inoculum that the appearance of disease in the following season depends. As might be expected, almost every disease has been noted in the literature on this subject, recent references to this point being 2, 7, 19, 70 and 122 among many others.

2. Given the inoculum, the conditions which determine its survival are probably the key to the subsequent appearance of disease, an epidemic of which is impossible without viable inoculum, in spite of any favorable circumstances in the current season. Although moisture has a considerable influence on the survival of fungus spores and bacteria, it is generally subservient to the influence of temperature. The literature on this subject, both prior to 1929 and subsequently, is voluminous and very interesting.

Vine mildew (*Plasmopara viticola*) commonly appears epidemically after wet winters (14, 15) but perhaps the warmer temperatures concomitant with the rains have an additional effect on the

abundant survival and germination of the fungus. A number of other Peronosporaceae are stated to be able to survive very low temperatures by means of their conidia, e.g., -12° C. for *Peronospora schachtii* (57). It seems, nevertheless, that in nature these conidia would not readily survive because the alternating low and warm temperatures, and dry and wet conditions, would sap their vitality much more severely than continuous low temperature. Most of these downy mildews usually survive by their oospores. Interesting work on the longevity of conidia of *Peronospora nicotianae*, *P. parasitica* and *Bremia lactucae* in Australia (1) demonstrated viability under dry conditions at low temperatures, especially if humidity was not too low. Conidia of the first fungus survived two months in cool, dry soil. While Australian conditions may allow overwintering by conidia, it may not be possible in other countries (126). Generally speaking, the rusts can withstand low temperatures (17, 19, 39, 70, 83, 92, 97).

Cereal rust epidemics in India provided an interesting problem and it has been demonstrated that temperatures influence the survival of the spores very thoroughly. *Puccinia glumarum* cannot withstand the high temperatures of the plains but survives the summer at high altitudes of and above 7,000 feet. On the other hand, *P. graminis* and *P. tritici* cannot survive the winter temperatures at these cold, high altitudes (65, 66). In the same way *Erysiphe graminis* (64) cannot survive the high temperatures of the plains and the annual re-occurrence depends on the survival of the conidia on self-sown plants at high altitudes. In America, Stewart's disease of corn (*Aplanobacter stewarti*) is severe only after warm winter months where the three months (December to February) mean temperature summation is over 100. This allowed the survival of the bacteria in sufficiently viable and distributed numbers to start an epidemic (99, 129).

An interesting fact relating to the survival of rust spores is the effect of ultra-violet light. It has been found that germination suffers if uredospores of *Puccinia graminis tritici* are exposed to direct sunlight or to ultra-violet rays and the rays from the red end of the spectrum. But this happened only when white and orange colored spores were used; those with red or greyish-brown walls do not suffer to such an extent and it is supposed that the red pigment when present protects the cytoplasm from the injurious light-

waves (28, 29). Ultra-violet light is also lethal to the mycelium of *Erysiphe graminis* (44).

3. The wind distribution of spores and bacteria has been known and accepted for most diseases but in some cases its importance has been over-estimated. With various bacteria and especially with *Venturia inaequalis* and *V. pirina*, wind seems to be negligible as a distributing agent until rain has detached the spores. There is no doubt, of course, that wind soon carries spores considerable distances but with the above fungi it was not sufficient to disturb the spores on the host tissues (107, 123). Wind velocities, artificially produced, of 300 to 500 m. per second were needed to detach scab conidia but only 60 m. per second were needed for *Cladosporium fulvum* and *Monilia fructigena* (121), while dropping water effected detachment very readily. This is a confirmation of the wind-blown rain experiments of Faulwetter in 1917 (see 33). Of course, rain does not only detach spores but also is a major factor in the expulsion of ascospores and pycnospores and is especially related to the presence of spores of *Venturia inaequalis* in orchards, the first appearance of which is the first clue for those responsible for the spray-warning service to be mentioned later (46, 110). (See also 33 for further details.)

The distribution of spores by wind, the use of aeroplanes in this study, and the various means for determining the presence of spores in the air, especially in crops and in orchards in relation to time of spraying, have been reviewed before (33). But it is of interest that spores have been recorded since even up to nearly 20,000 feet (69, 82) and that the air over the ocean is apparently free of spores (9), while the colder Arctic regions have very few spores (67, 68). In Russia, following the example of the United States and Canada (91), the aeroplane is being used to a considerable extent to examine the air for cereal rust spores (94). The aeroplane is also used in Great Britain and other countries for examining the fungal flora of the air. Cereals being tested for resistance to a rust form may be classed as resistant if no disease appears thereon. Whereas the case may really be that there are no spores of the rust in question in the air. Aeroplane exploration of the air to determine this point helps to form correct conclusions regarding resistance.

The rate of fall of spores in relation to wind distribution has

received attention for some time and calculations were made by McCubbin and Weston (see 33). Recently, Ukkelberg (111), using better apparatus, has tested the rate of fall of four cereal rusts and calculated their dispersal in a 30 mile per hour wind on the assumption of reaching 500 feet.

The epidemiology of cereal rusts is a subject on its own and cannot be adequately discussed in a few sentences. Only a few points have and can be raised herein but Stakman and Peltier have discussed this subject at length (79, 97).

DISEASE INITIATION AND EPIDEMICS

The initiation of disease and its development into an epidemic through the various stages of spore germination, infection, progress within the plant leading to collapse, production of secondary spores with their dispersal through the crop and finally the production of the over-wintering stage, all separately and collectively are bound up with meteorological conditions. The analysis of the numerous ways in which each of the factors influences the disease complex has been outlined before (33). Data on these points have accumulated to an overwhelming extent and cannot all be presented here. From the mycological papers published in the last six years which deal in any way with this subject (well over 600) only a few points can be mentioned.

It is very noticeable that much recent work on the germination of rust spores mentions, among other details, that better germination follows a scheme of freezing for several days, thawing, then wetting, perhaps followed again by drying and wetting (11, 50, 51, 100, 102). The exact scheme varies with the rust concerned but the idea remains the same (115). Some in investigating the black stem rust merely use naturally over-wintered material (92). Profuse germination of rust spores demands actual water and there is some reduction in the percentage germination in moisture saturated air or 99% and a great reduction below this degree of humidity (36, 42). Microscopic examination reveals a thin film of water round the spores in saturated air or 99% humidity. Very high humidity is also needed for the germination of other fungus spores (86, 116). It has been noted before (33) that many fungi, especially the rusts and downy mildews, need actual water for the germination of their spores and that a moisture saturated air was not

enough. Those writers who stated that 100% humidity was sufficient for germination probably had not examined for the presence on the spores of a thin film of water deposited in the saturated conditions—it probably was present. It is already known that spores dry out very quickly when exposed, the nature of the substratum influencing this considerably (53), but it is claimed that the germination of conidia of *Cystopus candidus* does not occur unless their own water-content becomes reduced by 50%. This is dependent upon the drying of the host tissues according to weather conditions (76). The same kind of relation is claimed for the conidia of potato blight (77). The temperature of production also influences the degree of germination; for example, *Puccinia graminis* teleutospores germinated better if produced at 55–60° F. than if produced at 70–75° F. (51). It is to be noted that very high humidities or saturated air are needed for infection and progress of disease, and this is generally true of downy mildews, potato blight and many Fungi Imperfecti (24, 113, 116).

There are several outstanding epidemics which are worth mentioning. Early blight of celery (*Cercospora apii*) depends on a combination of warm weather with heavy dew at night, no rain and light winds and, with the unusually high temperatures and relative humidity of 1931–32, the United States promptly suffered from a severe epidemic (98, 120). Mehta's work (64, 65, 66) on the cereal rust problem and cereal mildew has already been noticed in discussing the survival of spores. The occurrence of *Puccinia glumarum* each year at the foot of the hills has been correlated with the wind dispersal of uredospores from the infected self-sown plants in the hills, the uredospores being caught in aeroplane spore traps. The powdery mildew of the grape (*Uncinula necator*) in India is often epidemic in December when humidity and temperature is high but, in the districts where the monsoon is worse, the very heavy rains may check the intensity, though not the extensity, of the epidemic by washing off the infection (112).

The vine mildew (*Plasmopara viticola*) still continues to be a serious disease and is epidemic when continuous rains and temperatures of not lower than 13° C. prevail. High humidity does not seem sufficient for spore germination, an actual film of water being needed (14, 16, 74, 78, 85).

Apple scab (*Venturia inaequalis*) has been the subject of nearly

as much phenological research as potato blight and most of the recent work has aimed at obtaining data which could be used in a spray-warning service. The chief factor, perhaps, in this disease is the effect of early spring weather on the expulsion and germination of the ascospores, the production and germination of the conidia and the state of the leaves and buds. Wet periods long enough to produce the presence of spores in the air and to allow them to germinate, coupled with warm temperatures, lead to the initiation of an epidemic. While some state yet that the wind distributes the spores, others state that rain is the chief means of detachment of conidia, wind merely furthering the distance to which they may proceed. The whole phenological scheme fits in with the problem of when to spray to protect the susceptible tissues, usually the young, sappy tips just produced after heavy rains (40, 53, 62, 63, 72, 73, 121). Moore surveyed the phenology of this disease up to 1931 (72) referring to work already noted (33).

Potato blight (*Phytophthora infestans*) has been the subject of phenological research for a longer period than almost any other disease. Since Melhus put the biology of this fungus on sure ground, most of the work has either been a case of retesting or extending the scope of his discoveries or of applying them to the wider field of epidemics and the methods of forecasting their outbreak. Much of the literature has been noted (33) and Crosier (21, 22) has brought the subject almost up to date (1933), while his own researches have helped to complete some of the gaps in the knowledge of the biology of potato blight. Of particular interest is the study by Van Everdingen, using Miss Lohnis's material, in establishing a table of four requirements the fulfilment of which allowed a reasonable forecast of an epidemic of blight. These four conditions were: (1) a night temperature below dew point, of at least four hours' duration; (2) a night temperature not below 10° C.; (3) a mean cloudiness not below 0.8 on the following day and (4) rainfall of 0.1 mm., at least, on the following day. The Dutch Phytopathological Service succeeded in using Van Everdingen's four conditions for forecasting the liability of blight occurring and a spray-warning service has been in operation there since 1928. In Great Britain both Wiltshire (125) and Beaumont (4) have attempted to apply the Dutch rules for forecasting blight. But the detailed examination of meteorological data and the actual

outbreaks of blight showed that for that country the Dutch rules did not quite apply. Beaumont found that a better guide, in combination with the three other conditions, was a reading of the relative humidity at 3 p. m. instead of the night temperature below dew point. He was then able to correlate, in Devon, the incidence of blight with the occurrence of the four conditions through several years. As yet, however, a spray-warning service has not been established for this disease in Great Britain.

It is suitable to refer here to some serious attempts to place the science of the phenology of disease on a statistical basis. Tehon (105, 106) constructed graphs in which several meteorological factors could be used in combination and they indicated some promise; the writer has summarized the chief point in this work (33). There might be considerable use in Tehon's methods for some diseases and there is room for further investigation. The weak point in its use as a forecasting method is that for many, and usually the most important, diseases, the data used is too restricted and does not take into consideration the general biological facts, *e.g.*, to take two cases only, one, physiological strains of cereal rusts and their wind distribution, and two, the four conditions necessary for potato blight epidemics.

PHYSIOLOGICAL SPECIALIZATION

Before passing on to the question of spray-warning services, it is worth mentioning the relation of physiological specialization to this subject. It is well known that many rusts are very specific and also that specialization to a variety of a host is possible. *Puccinia graminis tritici* is not only limited to wheat but many of its strains are limited to certain varieties or sets of varieties. Reed (88) has reviewed this subject recently. Further, it has been found that infection by many of these rust strains is affected by weather. For example, a given wheat variety may be susceptible to a strain of *Puccinia graminis tritici* in summer but resistant in winter or it may be susceptible or resistant according to the stage the plant has attained, *i.e.*, seedling, vegetative or mature stages. Generally speaking, the temperature factor is the most important in this respect, though light and moisture have some influence. This subject is particularly important in the study of weather and disease, especially when this is designed to breeding new varieties

resistant in a given climate. In America, it is linked up with the aerial surveys for the presence or absence of certain rust spores at special times of the year in relation to the initiation and spread of epidemics. As Stakman points out, the discovery of spores in the air, blown from a district many miles away, is not necessarily a danger, unless the spores happen to be of a form or strain which will infect the particular variety of cereal crop which is being grown in that particular area (8, 37, 38, 43, 49, 52, 70, 75, 80, 90, 93, 96, 117, 119, 122).

PRACTICAL APPLICATION

There arises from the preceding discussion of epidemiology the question as to whether this increasing fund of knowledge can be used to control these diseases. It is now known that, for some diseases at least, given prompt meteorological and biological data, it is possible to forecast with reasonable accuracy the occurrence of an epidemic, though not the intensity or duration. A few countries have for some years developed an organization for the distribution of forecasts in relation to disease epidemics with the object of warning growers when to begin direct measures, such as spraying, against fungus and insect pests. The downy mildew of vines has been the subject of these spray-warning services for a long period and both France and Italy (60) have an extensive organization for this purpose. In only one of the vine districts of France, the number of subscribers using this organization is well above a thousand, a fact which demonstrates the usefulness of the service (128). Warnings are also given for powdery mildew and black rot of the grape, for apple scab and for potato blight. Holland's potato blight spray-warning service started in 1928 (125). In Canada and the United States, a spray-warning service against apple scab has now been in use for several years (20, 30, 81). Crosby gives a very detailed description of this organization as effected in New York State (20) and other states have services along the same lines. Of course, in the case of the spray-warning services in the United States, apple scab is only one of several troubles for which spray advice is given. There is little doubt but that this practical application of the research that has been carried out for years, on the phenology of diseases, will be extended to other diseases where control measures are possible both practically and economically.

FUNDAMENTAL RESEARCH

In most cases the exact manner in which the environmental factors influence the disease are not known but, for some, explanations have been obtained. One of the most interesting cases is that of seedling blight of wheat and maize (*Gibberella saubinetii*), which has been investigated by Dickson *et al.* (see 33). The fungus has a very wide temperature range and the disease in wheat is worse at high temperatures (16 to 18° C. according to variety), while in maize it is worse at low temperatures (8 to 16° C.). Wheat is naturally a cooler climate crop than maize and at low temperatures it was presumed that abundant carbohydrates allowed cell-wall thickening which thus conferred a measure of resistance. At high temperatures the low sugar and dextrin content prevented a rapid cellulose formation with consequent susceptibility. Maize, on the other hand, reverses this process, sugars being more abundant at high temperatures. Recently (27), maize seedlings which were produced resistant to seedling blight were found to contain some 20% more uronic acids (associated with polyglucuronides) than susceptible varieties at the lower temperatures. Similarly, the attack by *Fusarium herbarum* on wheat was correlated with the presence of xylan and other hemicelluloses; the higher the percentage of xylan, the more readily did the enzyme of the fungus destroy the cell-walls (35). Further, wheat attacked by *Puccinia glumarum* and *P. triticina* is usually more heavily infected at low temperatures and seems to be correlated with the increase of albumin at low temperatures (34). Ravaz (84) suggests that, by increasing the sap concentration of vines, resistance to mildew would be conferred. But in another publication (114) this contention is reversed, as sap concentrations were not less in the susceptible than in the resistant varieties, though it was higher in the more mature leaves on any individual plant.

Another case showing physiological phenomena is that of *Basisporium gallarum* on maize (87). Low temperatures in maize do not allow active translocation to start, as already shown in the case of seedling blight. It has been shown that this fungus enters the seed at low temperatures because, translocation from the embryo not having started, there is still a neutral reaction which is not toxic to the fungus. At higher temperatures, translocation commences at once with germination, whence the tissues become

acid and therefore toxic to the fungus, conferring an apparent resistance to the plant. There are some newer varieties which, being able to grow at low temperatures and therefore having an early translocation from the embryo, are resistant to the disease.

In fire-blight of pears, the development of the bacteria is correlated with high humidity. One of the points of infection and dissemination is the nectar—bees, etc., visiting here leave bacteria which rapidly increase therein and the nectar becomes a source of infection for the same plant and others. At high humidity, the bacteria increase rapidly in the nectar but fail to do so at low humidity. This is because at high humidity the sugar content is only 1 or 2%, whereas at low humidity it is as high as 55%; at the high sugar content the bacteria not only cannot develop but they also lose their virulence (108, 109).

An interesting point, perhaps indirectly associated with this subject, is the work on *Botrytis cinerea* which demonstrated that apparently new and permanent variations could be induced by the action of very high temperatures (3). Many other workers have induced variation in fungi by high temperatures, X-rays and other methods (3a). While in nature the same conditions could not exist, it nevertheless indicates a field of investigation as to the possibility of environment slowly changing the parasitism or saprophytism of a fungus. There are two small points worth mention. Some workers have recorded that the leaves of plants diseased at the roots were several degrees warmer than those of healthy plants, indicating decrease in water supply (31). Microclimate and other investigations in crops should take this kind of fact into consideration. Also, with the recent work which is fast developing on fungal antagonism in the soil, it will have to be made certain that conclusions on the influence of soil temperature, moisture and other factors should not rather have been based wholly or partly on this phenomenon.

The vast complexity of this subject, very generally reviewed above, indicates that more and more it will be imperative that the plant disease complex should not be investigated from the narrower view of the immediate cause. Teams, working in close combination and consisting of mycologist, pathologist, geneticist, physiologist, statistician, etc., will have better chances of elucidating the work which remains to be done than isolated mycologists.

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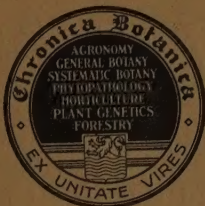
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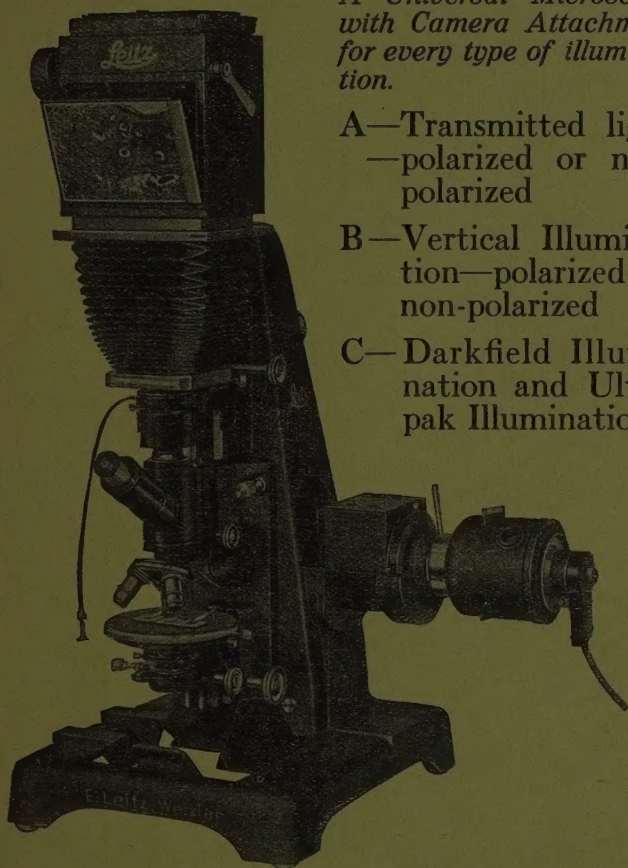
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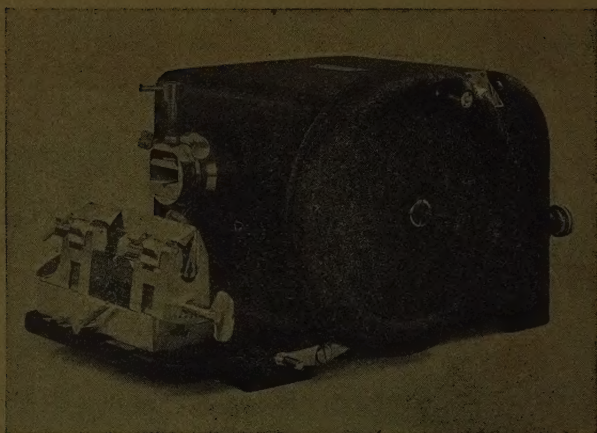
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